Factors determining territoriality in the strawberry poison-dart frog, *Dendrobates pumilio*

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Abstract: Territorial animals should allocate energy to defense based on the quality of their territory, which may be defined by the availability of resources such as food or sites for rearing offspring. The strawberry poison-dart frog, *Dendrobates pumilio*, inhabits tropical lowland wet forests in Costa Rica. *D. pumilio* is only reproductively active during the wet season (May-December), but males defend territories year-round. We hypothesized two explanations for territoriality among males during the dry season. First, territory quality may be defined by reproductive resources, i.e. the availability of bromeliads. Alternatively, optimal territories may be those containing the best access to food. We used measurements of perch height, snout-vent length, and male calling activity as putative surrogates for dominance. We used bromeliad abundance and mass relative to body length as measures of reproductive and nutritional resources, respectively. No measures of male dominance were related to either bromeliad abundance or food availability. Neither reproductive nor nutritional demands appear to influence territory selection and/or defense. These findings may indicate that there is no dominance hierarchy among males during the dry season, or that perch height, snout-vent length, and call attributes do not accurately indicate male dominance. Although there appears to be a territory structure during the dry season, it is still unclear what dictates this structure or why males expend energy by calling from their territories.

Key Words: dominance, bromeliads, reproduction, territory quality

Introduction

To maximize fitness, territorial animals should adjust their energetic investment in territory defense such that resource-rich territories will be defended most vigorously. Optimal territories should have high food availability, offer opportunities for reproduction, and/or provide shelter from predation. When these resources are limited, dominant individuals should preferentially inhabit the better territories and actively defend them.

The dominance structure of males may influence territory partitioning within populations of the strawberry poison-dart frog, *Dendrobates pumilio*, which lives in tropical lowland wet forests of Costa Rica. Although *D. pumilio* maintain territories year-round, they are only reproductively active during the wet season, from May to November. After eggs hatch, the females carry tadpoles to bromeliad tanks (phytotelmata) in the canopy, where the tadpoles develop. Intraspecific competition for reproductive opportunities, i.e. access to females, should result in the best territories being acquired by the most dominant males (Donnelly 1989). It is possible that reproductive resources, such as number and quality of bromeliads, may be indicators of territory quality year-round. Alternatively, because male territoriality is not restricted to the breeding season, other resources such as food abundance may be more important determinants of territory quality during the non-breeding season. In either case, as the quality of a territory increases, the resident male should be forced to expend more energy defending it from competitors, especially by calling, which occurs throughout the year.

We offer two hypotheses to explain the basis of territory defense in *D. pumilio* males during the dry season. Territory quality may be defined by 1) reproductive resources, i.e., the availability of bromeliads, or 2) food re-

sources. We predicted that male dominance, quantified by snout-vent length, perch height, and calling activity, would be positively correlated with either bromeliad abundance or mass residuals (a surrogate for food quality and accessibility), respectively.

Methods

On 17 and 19 February 2000, we measured the calling activity of 30 *D. pumilio* males within 1 km NW of the Estacion Biologica La Selva, Costa Rica, along the STR trail. We recorded the total amount of time spent calling, the average duration of each call, and the number of individual calls made during a 5 min period. We also measured staccato rate by haphazardly recording the number of staccato sounds during three 10 s intervals. We then captured each individual and recorded weight, snout-vent length (SVL), and perch height. Finally, we counted the number of bromeliads within each male's territory, which we defined as a circle (2 m in radius) centered around his initial position.

To determine the relative importance of nutritional resources in assessing territory choice, we used the residuals from a linear regression of mass versus SVL regression to represent male condition and therefore the availability of food resources in the territory. A measure of composite call value was generated using a principle components analysis of staccato rate, time spent calling/5 min period, mean duration of call, and number of calls/5 min period. We interpreted PC1 as a representation of a male frog's calling activity, or composite call rate (Table 1). Mean ± SD for physical characteristics of the frogs, as well the four measurements comprising composite call rate, are given in Table 2. We tested for interrelationships between all variables using a correlation matrix. We used separate regression models to examine the effects of SVL, perch height, and calling activity on our two measures of territory quality, bromeliad abundance and mass residuals. Bromeliad abundances were log transformed ($\log_{10}(x + 1)$).

Table 1. Results from principle components analysis of four measurements of calling activity in *D. pumilio* frogs at La Selva Biological Station, Costa Rica. Loading scores are from the first principle component axis and indicate the direction and relative contribution of individual characteristics. The cumulative percent describes the amount of total variance explained by the PC axis.

Characteristic	Loading Score
Call rate	0.50
# Calls / 5 min	0.15
Call length	0.57
Proportion of time calling	0.64
Cumulative %	49.03

Table 2. Means and standard deviations of all characteristics measured on 30 *D. pumilio* males at La Selva Biological Station, Costa Rica.

Variable	Mean	SD
S-V length (mm)	19.95	0.96
Mass (g)	0.73	0.09
Perch height (cm)	21.40	16.69
# Bromeliads	21.17	42.37
Call rate (calls / s)	5.03	9.54
# calls	3.57	1.76
Call length (s)	31.55	14.03
Proportion of time calling	0.33	0.16
Residual mass (g)	0.00	0.08

Results

Body size was correlated with two measurements of calling activity: call rate and proportion of time calling per 5 min period. Perch height was positively correlated with the number of calls per 5 min period and call rate was positively correlated with number of nearby bromeliads (Table 3).

There were no relationships between our indicators of male dominance (SVL, composite call value, and perch height) and number of bromeliads in a territory (Fig. 1; $r = 0.24$, $p = 0.20$; $r = 0.18$, $p = 0.35$; and $r = 0.27$, p

Table 3. Correlations between all measured variables on *D. pumilio* at La Selva Biological Station, Costa Rica. Call rate was calculated by averaging the number of staccato sounds per three 10 s intervals. Number of calls, call length, and proportion of time calling were calculated per 5 min study period.

Variable	A	B	C	D	E	F	G	H
A. S-V length								
B. Perch Height	0.19							
C. # Bromeliads	0.15	-0.19						
D. Call rate	0.35	0.15	0.46					
E. # Calls	0.09	0.22	-0.10	0.03				
F. Call length	0.14	-0.15	0.16	0.41	-0.32			
G. Proportion of time calling/5 min	0.33	0.05	0.04	0.38	0.49	0.61		
H. Mass residuals	0.02	0.01	-0.26	0.06	-0.04	-0.03	0.06	
I. Composite call value (PC I)	0.34	0.04	0.24	0.70	0.21	0.80	0.89	0.03

= 0.49, respectively; n = 30 frogs in all cases). The mass residual of each male was also independent of SVL, call activity, and perch height (Fig. 1; r = 0.02, p = 0.92; r = 0.03, p = 0.87; r = 0.01, p = 0.94, respectively).

Discussion

Our results may indicate that neither bromeliad abundance nor food resources are important factors in determining territory quality, or that territory occupation is not based upon male dominance structures. Other factors relevant to reproductive success, such as bromeliad size and height from the forest floor, or simply male condition, may be more relevant than bromeliad abundance in the assessment of habitat quality. The range of a female territory is larger than a male territory (Donnelly 1989), implying that a female is not solely restricted to the reproductive resources within a single mate's territory. Therefore bromeliad abundance may not necessarily determine the reproductive success of males.

Male body mass relative to body length (residuals from regression) was not related to any measures of male dominance, suggesting that the diets of dominant versus subordinate males do not differ. Previous research supports the idea that food may not be a limiting resource for *D. pumilio* frogs at La Selva (Robakiewicz 1992). However, the seasonality of La Selva may still create variation in prey abundance, with higher numbers occurring during the wet season. This study took place at the beginning of a dry season with unusually high rainfall, which may have resulted in the maintenance of high prey populations into the dry season.

Alternatively, it is possible that territory occupation is not based upon male dominance structures. If food resources are not limited and reproductive resources do not exert year-round pressure upon territory selection, males may not need to actively defend their territory against other males. Instead, because there is very little difference in territory quality, males may distribute themselves at random with respect to male size, aggressiveness, and potential position in a dominance hierarchy. This would still afford the benefits of preventing physical interactions that may be even more energetically costly than calling.

Our results challenge the assumption that territory quality is defined by resource availability within a habitat. If territoriality exists in *D. pumilio* populations during the dry season, there should be benefits that at least balance the costs of defending a territory. The benefits of maintaining a territory into the wet season, when reproductive benefits accrue,

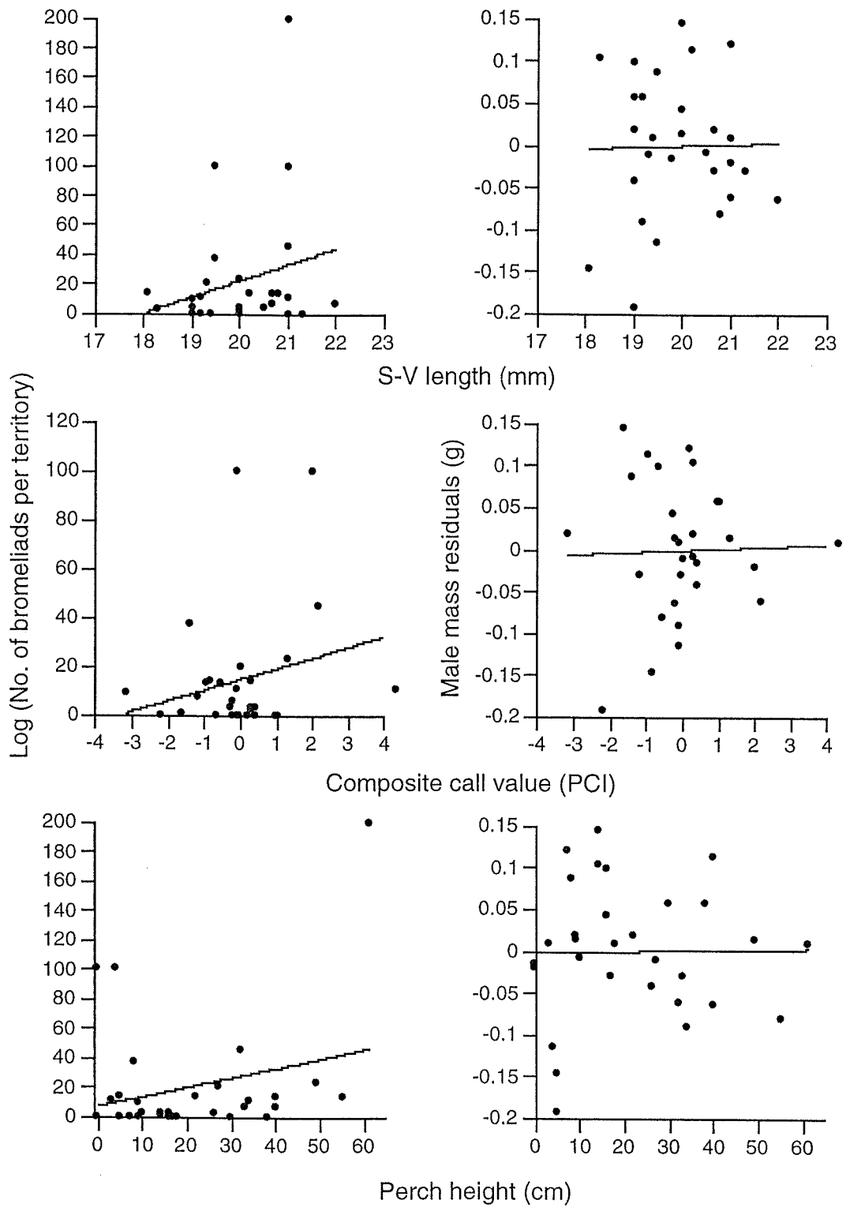

Figure 1. Number of bromeliads per territory (left) or mass residuals of males (right) as a function of three putative indicators of male dominance; snout-vent length, composite call value, and perch height, in a population of *D. pumilio* frogs at La Selva Biological Station, Costa Rica. Mass residuals were calculated from regressions of mass versus SVL. Composite call value represents a synthetic variable of four measurements of calling activity (1st axis of a principal components analysis; Table 1).

may validate its defense throughout the year. Additional studies could test for this and other possible benefits for *D. pumilio* of territoriality during the non-reproductive season.

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